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Legacies of past land use challenge grassland recovery – An example from dry grasslands on ancient burial mounds

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Abstract

Due to large-scale agricultural intensification, grasslands are often restricted to habitat islands in human-transformed landscapes. There are approximately half a million ancient burial mounds built by nomadic steppic tribes in the Eurasian steppe and forest steppe zones, which act as habitat islands for dry grassland vegetation. Land use intensification, such as arable farming and afforestation by non-native woody species are amongst the major threats for Eurasian dry grasslands, including grasslands on mounds. After the launch of the Good Agricultural and Environmental Condition framework of the European Union, in Hungary there is a tendency for ceasing crop production and cutting non-native woody plantations, in order to conserve these unique landmarks and restore the historical grassland vegetation on the mounds. In this study, restoration prospects of dry grassland habitats were studied on kurgans formerly covered by croplands and *Robinia pseudoacacia* plantations. Soil and vegetation characteristics were studied in the

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spontaneously recovering grasslands. The following questions were addressed: 1; How does site history affect the spontaneous grassland recovery? 2; Do residual soil nutrients play a role in grassland recovery? In former croplands, excess phosphorus, while in former *Robinia* plantations, excess nitrogen was present in the soil even four years after the land use change and grassland vegetation was in an early or mid-successional stage both on the mounds. The results showed that, without proper management measures, recovery of grassland vegetation is slow on mounds formerly used as cropland or black locust plantation. However, restoration efforts, focused on the restoration of mounds formerly covered by croplands, can be more effective compared to the restoration of mounds formerly covered by forest plantations.

Keywords
cropland, grassland restoration, kurgan, nitrogen, phosphorus, *Robinia pseudoacacia*, soil, steppe

Introduction

In intensively used agricultural landscapes, the remaining natural and semi-natural habitats often occur on small natural features (SNFs). Many of SNFs, such as verges, field margins and midfield islets are physically inappropriate for agricultural utilisation (Lindborg et al. 2014; Jakobsson et al. 2018; Fekete et al. 2019). Other types of SNFs have religious or cultural importance, which prevented their agricultural utilisation (Dudley et al. 2009; Molnár V. et al. 2017; Löki et al. 2019). Amongst them, ancient burial mounds (also called kurgans) of the Eurasian steppe and forest steppe regions are of particular importance (Sudnik-Wójcikowska et al. 2011; Bede et al. 2015; Bede and Csathó 2019; Deák et al. 2016a, 2019; Dembicz et al. 2018). They are earthen mounds of a few metres height, which were constructed from the topsoil layers of the surrounding areas by nomadic steppic tribes several millennia ago, mainly for burial purposes (Dembicz et al. 2016; Lisetskii et al. 2016). The estimated number of these mounds is more than 600,000 in Eurasia and they are typical landscape elements from Hungary to Mongolia (Deák et al. 2016a, 2019). A considerable proportion of these mounds still hold grassland vegetation; hence, mounds are valued as being stepping stones or biodiversity hotspots for grassland specialist plant and animal species even in transformed agricultural landscapes (Bede and Csathó 2019; Tóth et al. 2019; Deák et al. 2020). Despite their cultural importance and steep slopes, many of the mounds have been exposed to ploughing and afforestation works in the past centuries (Deák et al. 2016a, b). Restoration of their former vegetation is an important task for nature conservation (Valkó et al. 2018). Such restoration projects can increase the habitat area of dry grasslands, create stepping stones for grassland specialist species and the restored mounds can be used as demonstration sites for environmental education (Valkó et al. 2018).

The Cross-Compliance system of the European Union Common Agricultural Policy is a progressive initiative that contributes to a more environmental-friendly agriculture. One of its pillars is the Good Agricultural and Environmental Condition framework, which contributes to the development of a long-term and ecologically sustainable agricultural environment (Brady et al. 2009). As there are more than 1600

ancient steppic burial mounds in Hungary (Tóth 2006), that is why they were selected as the landscape elements typical to the country according to the GAEC regulations. Due to this, now there is a tendency for the cessation of crop production on the mounds and sometimes also in a surrounding buffer zone (Rákóczi and Barczi 2014; Tóth et al. 2018). For reconstructing the original vegetation of these important landscape elements, national park directorates and NGOs are increasingly involved in the restoration of grasslands on mounds (Valkó et al. 2018). As part of this initiative, black locust plantations have been cut on many mounds in order to reconstruct the historical landscape and increase the landscape value of the mounds. However, due to limited capacity and financial resources, in most of the cases the abovementioned favourable land use changes on mounds (i.e. cessation of crop production and cutting of non-native plantations) were not followed by any other restoration measures; thus the grasslands are recovering spontaneously. Another challenge is the isolated situation of the mounds: most of them are surrounded by arable fields, therefore, post-restoration management by grazing or mowing is particularly challenging (Deák et al. 2020).

In grassland restoration, spontaneous recovery became increasingly acknowledged (Prach and Řehounková 2008; Török et al. 2011a). In many cases, it is the best option, because it is a natural method, it has low costs and if proper propagule sources of target species are present, successful grassland recovery can be expected (Hedberg and Kotowski 2010; Kiehl et al. 2010). Promising examples of spontaneous grassland recovery were reported from many parts of Central and Eastern Europe, such as the Czech Republic (e.g. Prach and Řehounková 2008; Lencová and Prach 2011, Jírová et al. 2012), Hungary (e.g. Csecserits and Rédei 2001; Csecserits et al. 2011; Török et al. 2011b; Albert et al. 2014) and Romania (e.g. Ruprecht 2005, 2006). However, on isolated sites where propagule sources are limited, vegetation development may stall at a stage dominated by weeds (Prach and Pyšek 2001; Matus et al. 2003).

Here we study two scenarios of grassland recovery: recovery on former croplands and former plantations on mounds. Ploughing and afforestation are responsible for the reduction of grassland area and decline of grassland species richness in many parts of Eurasia (Deák et al. 2016a, b; Biró et al. 2018). Loess grasslands on fertile chernozem soils were the most severely affected by conversion to croplands or plantations (Biró et al. 2018). Amongst plantations, the North-American invasive black locust (*Robinia pseudoacacia* L., Fabaceae) represents a large conservation problem due to its high persistence, excellent vegetative and generative spread, intense evaporation and competition for resources, shading and nutrient accumulation effects, which all lead to the degradation and disappearance of the formerly typical grassland vegetation (Vítková et al. 2017).

The objective was to evaluate the prospects for restoring grasslands in degraded (ploughed and planted with black locust) ancient burial mounds, in order to provide information that will support the development of management plans, restoration and conservation of the local biota. We asked the following questions: 1; How does site history affect the spontaneous grassland recovery? 2; Do residual soil nutrients play a role in grassland recovery? Our final goal was to give recommendations for the restoration of grasslands on variously degraded burial mounds.

Material and methods

Study sites

We studied soil and vegetation of six mounds situated in the Hortobágy National Park, EastHungary (Figure 1). Climate conditions are warm temperate, fully humid, with hot summers (Kottek et al. 2006), the calculated annual mean temperature for the area between 1961 and 2010 is 10.7 °C, the average annual precipitation is 544 mm (Lakatos et al. 2013). The area is in the Great Hungarian Plain, dominantly consisting of Pleistocene-Holocene alluvial silt and clay, mixed with aeolian dust. The surface is plain (86–89 m a.s.l.), with nearly negligible elevation differences, being < 1–2 m km^{-2} on average, from which the studied mounds rise 3–6 metres above the surrounding landscape. The mounds were built using soil material collected from the topsoil layer of the neighbouring areas around several thousands of years ago. The mounds are always located on the highest position of the landscape, their surrounding being typically covered by chernozemic soils. The classification status of the soils of these landscapes according to the World Reference Base range from Chernozems over Kastanozems to Phaeozems, depending on the topsoil aggregate quality and the subsoil's carbonate status. The typical natural habitat types in the region are alkaline wetlands in the lowest elevation, alkaline dry grasslands at medium and dry loess

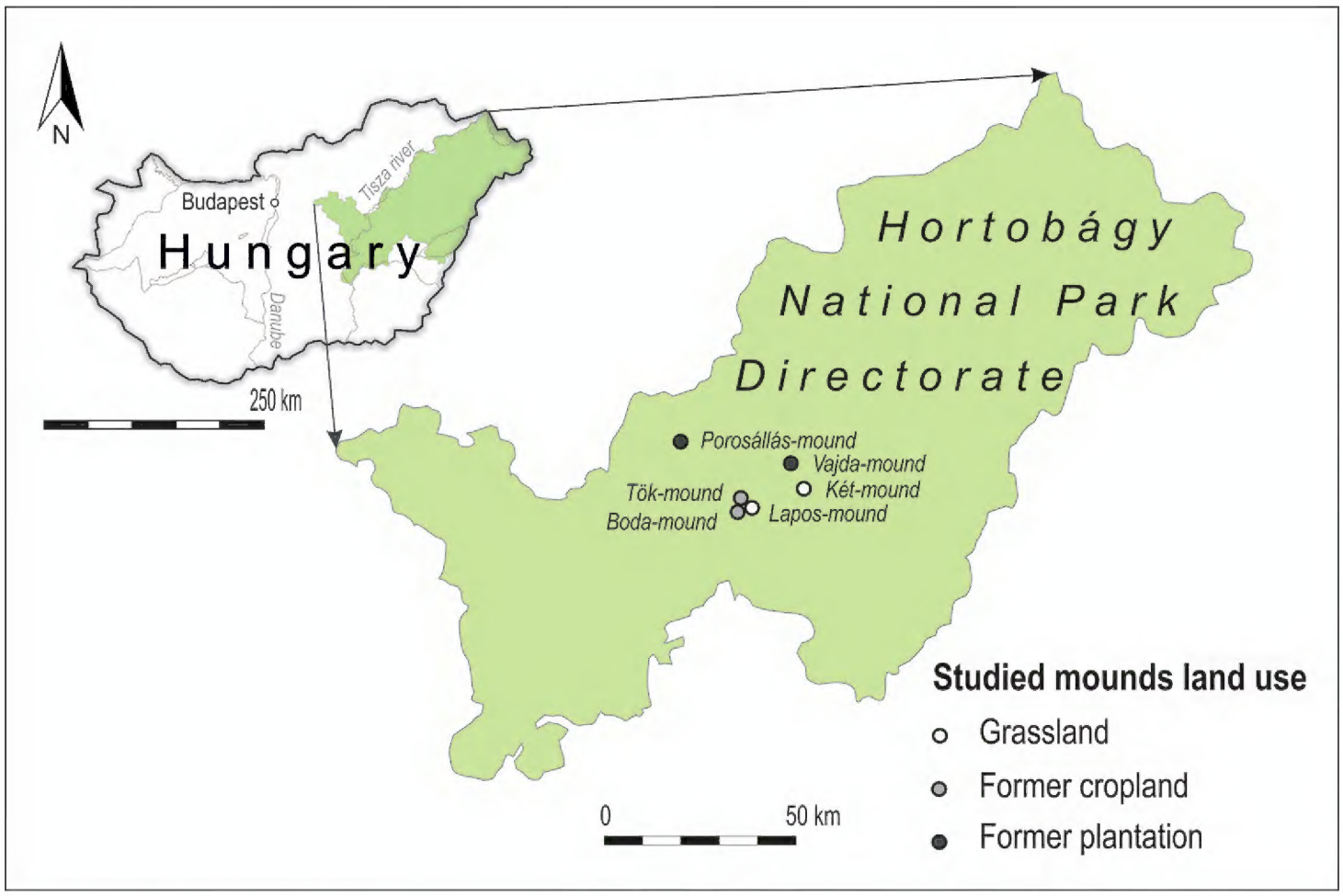

Figure 1. Study area: location of the studied mounds.

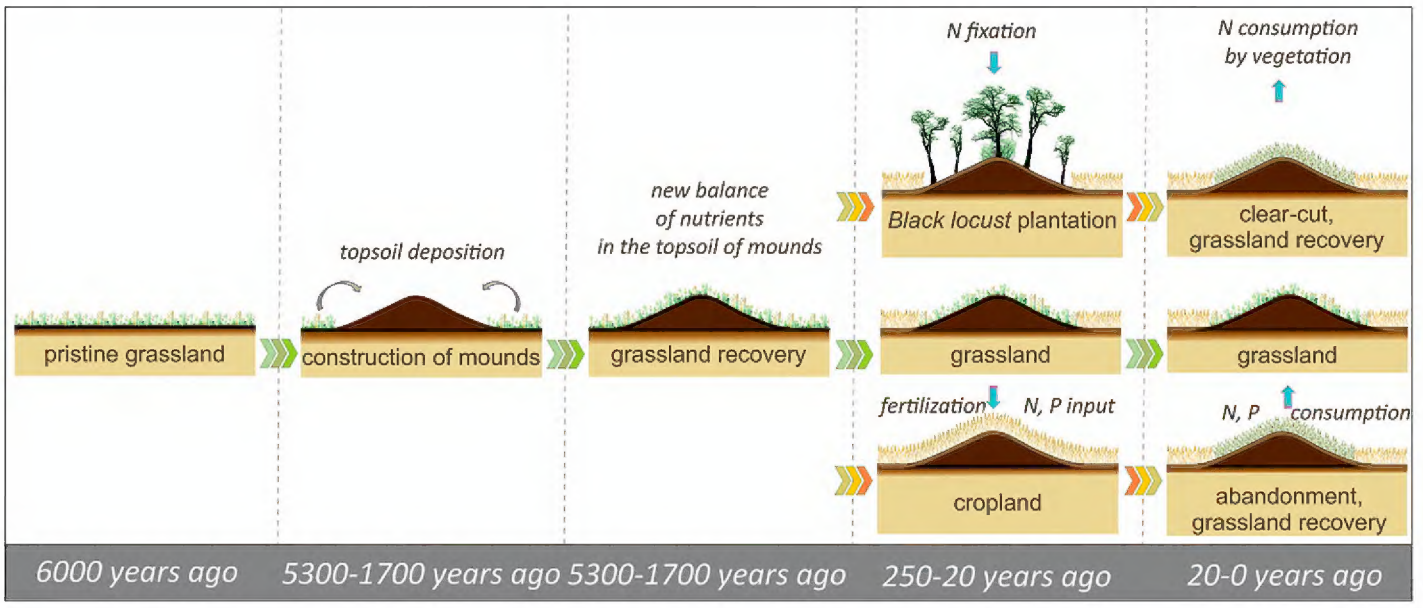

Figure 2. The soil and vegetation development of the studied mounds.

grasslands at the highest-elevated areas (Deák et al. 2014). Besides natural habitats, there are several croplands in the national park, where cereals, alfalfa and maize are the most typical crops. The majority of croplands are managed in an extensive way as farmers manage their lands according to the regulations of agri-environmental schemes, which limit the use of chemicals.

The vegetation of four surveyed mounds was formerly seriously degraded: two mounds (Porosállás- and Vajda-mounds) were formerly covered by black locust (*R. pseudoacacia*) plantations and two mounds were used as arable fields (Boda- and Tök-mounds). According to the oldest available orthophotos, all the two mounds with former croplands were already ploughed and the two mounds with *Robinia* plantations were already afforested in 1961. Based on archive descriptions, we can estimate that afforestation lasted for at least 80 years and crop production for at least 200 years on the studied mounds. Spontaneous grassland recovery started in 2012 in all sites: plantations have been cut and ploughing was stopped. As reference, we selected two mounds (Kettős- and Lapos-mounds) with well-preserved pristine grassland vegetation. Figure 2 shows the land use changes and the related processes of soil and vegetation development in the study sites in the past 6000 years.

Field sampling

Soil conditions were sampled in ten randomly distributed 1 m × 1 m permanent plots on each mound. From each plot, three subsamples were collected with 100 cm^3 stainless steel sampling cylinders, representing the uppermost 5 cm of the soil. First soil sampling was carried out in late June 2014 and it was repeated in late June 2016. On each mound, we designated ten 1 m × 1 m plots (altogether 60 plots), in which we recorded the percentage cover of vascular plant species in June 2016.

Laboratory analyses

Soil subsamples from the same plots and same year were then mixed and, after homogenisation, dried at 40 °C until weight constancy (approximately three days). In the laboratory, pH (H_2O; KCl), plant available nitrogen content and plant available phosphorus content were measured. Soil pH was measured with standard glass electrode in 1:2.5 suspensions prepared with water (pH_{H2O}), and KCl solution (pH_{KCl}), respectively (MSZ-08-0206:1978 2.1). Plant available P was determined after extraction with 0.1 M ammonium-lactate solution buffered with 0.4 M acetic acid at pH 3.7. Plant available NO_3^--N was extracted with 1 M KCl solution. Both N and P content of extracts were determined by spectrophotometric measurements, according the Hungarian standards (MSZ 20135 1999).

Data processing

We calculated cover-weighted scores of Ellenberg ecological indicator values for water (WB), nutrient (NB) and light (LB) adapted to the Hungarian conditions (Borhidi 1995). Based on the social behaviour type (SBT) system of (Borhidi 1995), we categorised the species into two ecological groups, grassland species and weeds. We considered specialists (S), generalists (G) and competitors (C) as grassland species and adventive competitors (AC), ruderal competitors (RC) and weeds (W) as weeds. The SBT system assigns a naturalness value to each category, ranging from -3 (AC) to +6 (S). We calculated the cover-weighted mean naturalness index for each plot, to characterise the overall naturalness.

For visualising the vegetation patterns on the mounds with different site history, we used Detrended Correspondence Analysis (DCA), based on specific cover scores. Soil nitrate and phosphorus content were included as overlay (CANOCO 5; ter Braak and Šmilauer 2012). We performed indicator species analysis to identify species confined to mounds with a certain site history (Dufrêne and Legendre 1997). For the analyses, we used the 'labdsv' package (Roberts 2019) in an R environment (R Core Team 2020).

To explore the effects of 'site history', time since grassland recovery started ('year') and their interaction (explanatory variables) on soil pH ($pH_{(H2O)}$; $pH_{(KCl)}$), soil nitrate and phosphorus content (dependent variables), we used Repeated Measures General Linear Models (RM GLMs) accounting for the normal distribution of the dependent variables (Zuur et al. 2009). Scores of soil variables were log-transformed to approximate them to normal distribution. We used the Greenhouse-Geisser correction for calculating degrees of freedoms and Tukey's test for calculating post-hoc pair-wise comparisons.

We used Generalised Linear Mixed Models (GLMMs) to explore the effects of 'site history' and two soil parameters ('soil nitrate content' and 'soil phosphorus content') (explanatory variables) on the naturalness index, ecological indicator values and the species richness and cover of grassland species and weeds in 2016 (dependent variables). The ID of the 'study sites' was included in the models as a random factor. Scores of naturalness index, ecological indicator values and cover of grassland and weed species were log-transformed to approximate them to normal distribution. Species number of grassland specialists and weeds were fitted using Poisson distribution with a log

link. We used Tukey's test for calculating post-hoc pair-wise comparisons. The RM GLMs and GLMMs were calculated using IBM SPSS Statistics v. 22 programme (Armonk, NY: IBM Corp). Significance level was set at $p \leq 0.05$.

Results

Soil characteristics

We did not detect any difference in the soil $pH_{(H2O)}$ and $pH_{(KCl)}$ of the studied mounds (Table 1). The highest values for both $pH_{(H2O)}$ and $pH_{(KCl)}$ were recorded in the former croplands in 2014, but the difference between mounds with different history was not significant (Figure 3). Site history had a significant effect on plant available soil N content (NO_3^-). N content was the highest in former black locust plantations and the lowest in former croplands. Plant available soil P content was affected by time since grassland regeneration started ('year') and 'site history' (Table 1, Figure 3). P content was the highest in former croplands and the lowest in former black locust plantations.

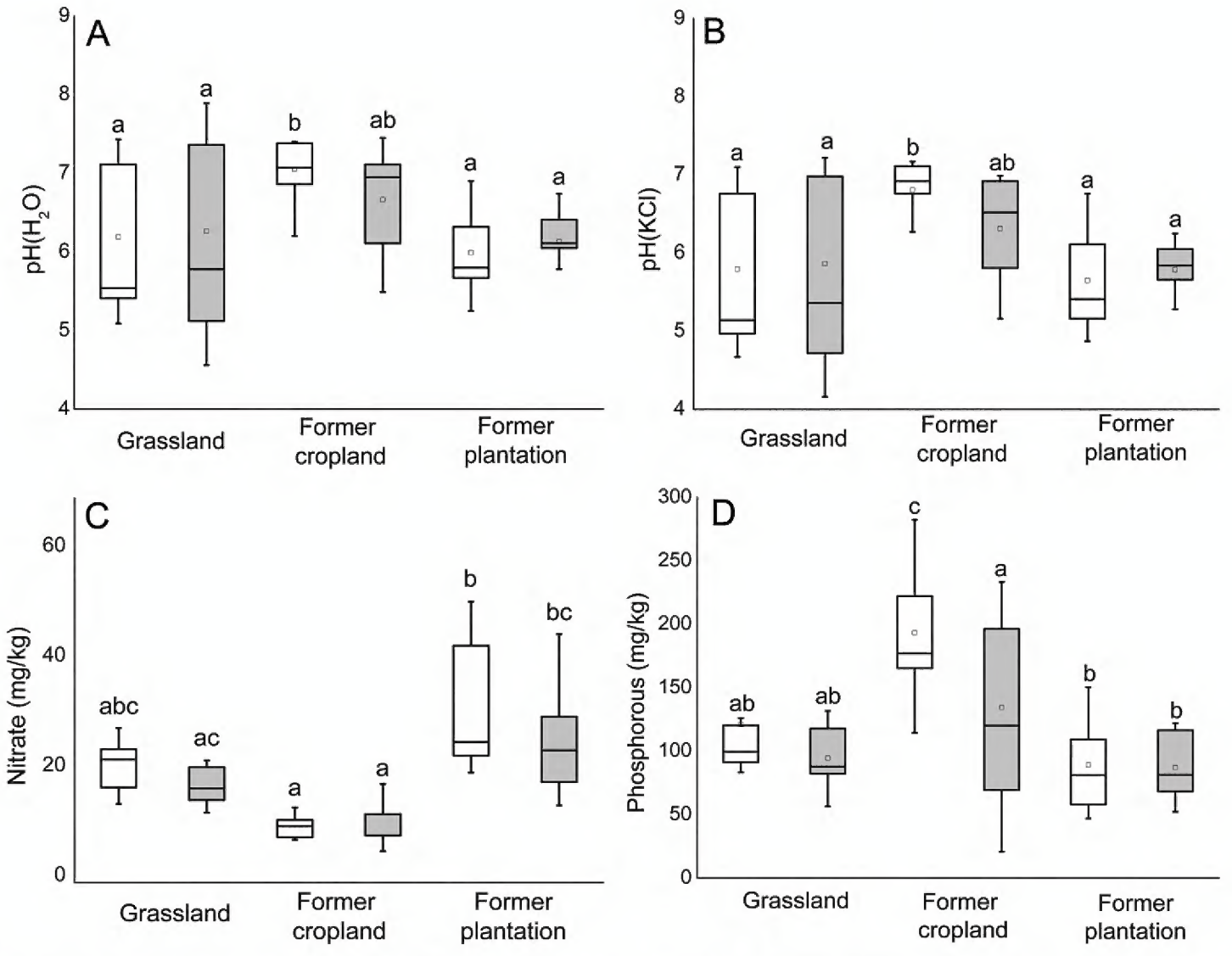

Figure 3. Soil characteristics (A – $pH_{(H2O)}$, B – $pH_{(KCl)}$, C – NO_3^--N content and D – P content (P_2O_5)) measured in the studied mounds (grasslands, former croplands and former plantations). White boxes represent data from 2014, grey boxes represent data from 2016. Different letters indicate significant differences between groups (Tukey test, $p \leq 0.05$).

Table 1. Effects of site history, year and their interaction on soil attributes (RM GLM). Notations: *** p < 0.001; ** p < 0.01; * p < 0.05; n.s.: non-significant.

Parameter	Site history				Year				Site history × Year			
	df_{num}	df_{den}	F	*p*	df_{num}	df_{den}	F	*p*	df_{num}	df_{den}	F	*p*
$pH_{(H2O)}$	2	1.067	2.636	n.s.	1	1	0.425	n.s.	2	1.247	1.426	n.s.
$pH_{(KCl)}$	2	1.088	2.822	n.s.	1	1	1.080	n.s.	2	1.323	1.972	n.s.
NO_3^--N content	2	1.467	37.289	***	1	1	2.190	n.s.	2	1.331	0.138	n.s.
P content (P_2O_5)	2	1.730	10.592	**	1	1	17.590	**	2	1.363	3.120	n.s.

Table 2. Results of indicator species analyses of the vegetation of mounds with different site history. Notations: G – mounds covered by grassland; A – mounds formerly covered by arable land; P – mounds formerly covered by *Robinia* plantation; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Species	Site history	Indicator value	p	Frequency
Carex praecox Schreb.	G	0.55	***	11
Koeleria cristata (L.) Pers. em. Borbás ex Domin	G	0.49	***	14
Salvia nemorosa L.	G	0.40	***	8
Festuca pseudovina Hack. ex Wiesb.	G	0.40	**	13
Elymus hispidus (Opiz) Melderis	G	0.35	**	7
Arenaria serpyllifolia L.	G	0.33	*	18
Plantago lanceolata L.	G	0.32	**	8
Bromus hordeaceus L.	G	0.32	*	14
Trifolium retusum L.	G	0.30	**	6
Euphorbia virgata Waldst. et Kit.	G	0.30	***	6
Erodium cicutarium (L.) L'Hér.	G	0.26	*	8
Eryngium campestre L.	G	0.25	*	5
Trifolium striatum L.	G	0.25	**	5
Stipa capillata L.	G	0.20	*	4
Cerastium semidecandrum L.	G	0.20	*	4
Bromus tectorum L.	A	0.84	***	18
Torilis arvensis (Huds.) Link	A	0.49	***	12
Convolvulus arvensis L.	A	0.44	*	34
Alopecurus pratensis L.	A	0.43	***	12
Achillea collina Becker ex Rchb.	A	0.42	**	18
Veronica arvensis Murray	A	0.34	**	8
Geranium molle L.	A	0.26	*	9
Xanthium strumarium L.	A	0.25	**	5
Vicia grandiflora Scop.	A	0.20	*	4
Lolium perenne L.	A	0.20	*	4
Elymus repens (L.) Gould	P	0.65	***	30
Ballota nigra L.	P	0.51	***	14
Bromus sterilis L.	P	0.35	***	7
Silene alba (Mill.) E.H.L. Krause	P	0.28	*	11
Galium aparine L.	P	0.26	*	13
Conium maculatum L.	P	0.20	*	4

Vegetation

We found altogether 92 vascular plant species on the studied mounds. Total species numbers were 64 in the grasslands, 50 in the former croplands and 24 in the former plantations. The vegetation composition of mounds with a different site history was well separated on the DCA ordination (Figure 4). We detected a considerable difference between the vegetation of the two mounds covered by grasslands.

Indicator species of grasslands were *Carex praecox* Schreb., *Koeleria cristata* (L.) Pers., *Salvia nemorosa* L. and *Festuca pseudovina* Hack. ex Wiesb. (Table 2). Typical species of former croplands included *Bromus tectorum* L., *Torilis arvensis* (Huds.) Link, *Convolvulus arvensis* L., *Alopecurus pratensis* L. and *Achillea collina* Becker ex Rchb. Former black locust plantations were characterised by *Elymus repens* (L.) Gould and *Ballota nigra* L. (Table 2).

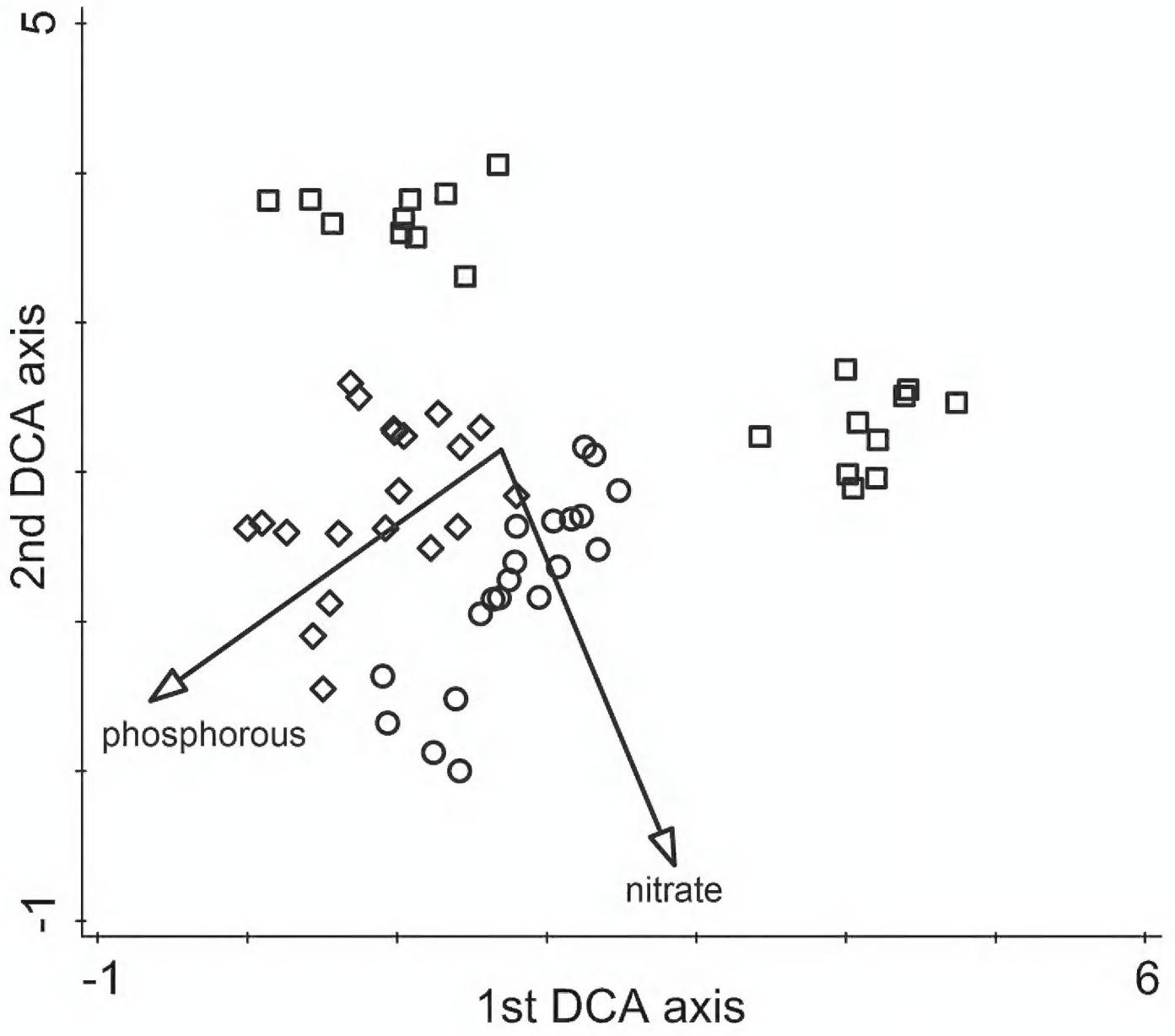

Figure 4. DCA plot of the vegetation of study sites, based on the species composition. Soil nitrate and phosphorus content were included as an overlay. Notations: squares – grasslands; diamonds – former croplands, circles – former plantations. Eigenvalues were 0.753 and 0.548 for the first and second axis, respectively. Cumulative explained variance of the first and the second axis were 12.72% and 21.98%, respectively.

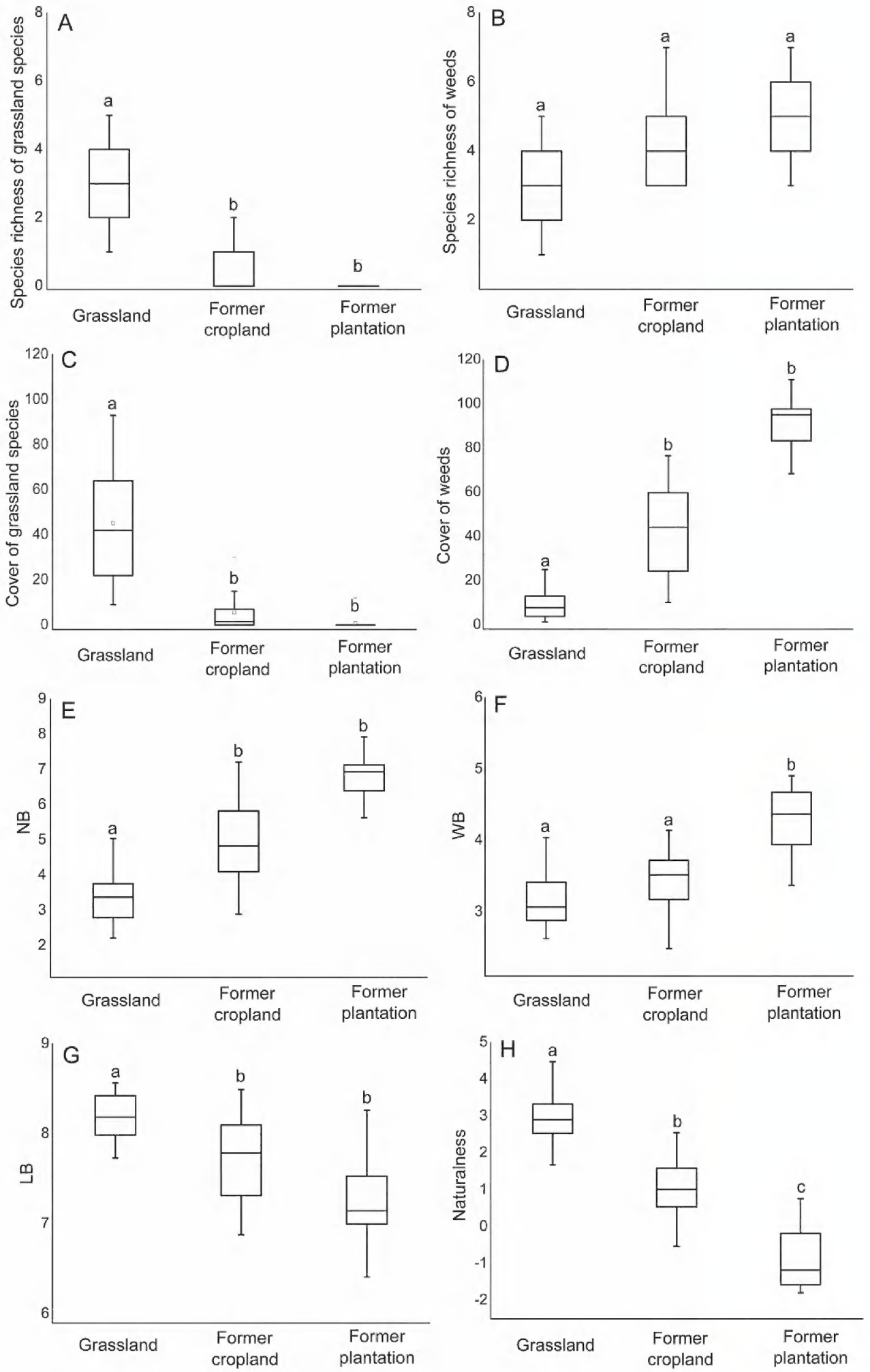

Figure 5. Vegetation characteristics in the studied mounds (grasslands, former croplands and former plantations): **A** species richness of grassland species **B** species richness of weeds **C** cover of grassland species **D** cover of weeds **E** cover-weighted ecological indicator scores for nutrients (NB) **F** cover-weighted ecological indicator scores for water (WB) **G** cover-weighted ecological indicator scores for light (LB) **H** naturalness score. Different letters indicate significant differences between groups (Tukey test, $p \leq 0.05$).

Table 3. Effects of site history, soil nitrate and phosphorus content on the vegetation characteristics of the studied mounds (Generalised Linear Mixed Models). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s., non-significant. Notations: NB, WB, LB: cover-weighted means of ecological indicator values for nutrients, water and light, respectively.

	Site history		Nitrate		Phosphorus	
	F	p	F	p	F	p
Naturalness	46.35	***	5.15	*	5.40	*
Species richness						
Grassland species	17.59	***	0.19	n.s.	1.80	n.s.
Weeds	1.95	n.s.	0.61	n.s.	0.61	n.s.
Cover						
Grassland species	17.74	***	0.20	n.s.	3.09	n.s.
Weeds	70.27	***	0.03	n.s.	0.01	n.s.
Ecological indicator values						
NB	9.02	***	0.93	n.s.	1.19	n.s.
WB	7.97	***	2.51	n.s.	0.44	n.s.
LB	21.38	***	13.09	***	3.25	n.s.

The re-sprouting ramets of the black locust were only present in the plots of the Vajda-mound and the average cover of black locust was 0.9% in the plots.

Site history significantly affected the naturalness of the vegetation, it was the lowest in former plantations and the highest in grasslands (Table 3, Figure 5). Soil nitrate content decreased the naturalness of the vegetation (coefficient = -0.068; t = -2.324; GLMM), whilst soil phosphorus content increased it (coefficient = 0.010; t = 2.269; GLMM). Both cover and species richness of grassland species were affected by site history; their scores were significantly lower in former plantations and croplands. Cover of weeds was affected by site history; it was the highest in former plantations. Cover-weighted NB, WB and LB scores were affected by site history. Cover-weighted NB scores were higher in former plantations and croplands compared to grasslands. Cover-weighted WB scores were the highest in former plantations. Cover-weighted LB scores were the highest in grasslands.

Discussion

Soil characteristics

We found that pH was highest, close to 7 or even greater, in former cropland in 2014. The likely reason for this is that, in croplands, there was no organic matter accumulation on the surface and the surficial soil layer was constantly mixed with subsoil and the subsoils' carbonate saturation status was always higher in these soils than at the surface. During the study period, pH was not changed significantly in any of the mounds, but a slight increase in former plantation and slight decrease on former cropland could

be detected. Soil pH was much more heterogeneous in the grasslands compared to the former croplands and plantations. This supports the findings of the Penksza et al. (2011), Deák et al. (2016a,b) and Lisetskii et al. (2016) who emphasised the role of environmental heterogeneity in driving the plant diversity on steppic burial mounds. Heterogeneity of pH can be an important driver of small-scale plant diversity (Moeslund et al. 2013).

Plant available N content was the lowest in the former cropland and its amount did not change by time since abandonment. This is due to the additive effect of the depletion of soil N stocks by decades-long cultivation and the slow soil N-recovery during secondary succession (Matamala et al. 2008; An et al. 2019). Besides being a limiting factor for the establishment of grassland plant species, limited availability of soil N stocks may also limit the development of the vegetation by suppressing microbial decomposition and soil carbon sequestration (Knops and Tilman 2000). The highest N content was measured in former plantations as a legacy of the former presence of the black locust. By the enhanced nitrogen-fixing of the black locust and the decomposition of its nitrogen-rich leaves, the soil of these former plantations had a high N content (Bolat et al. 2015). Although we detected a slight decrease in soil N content after the plantation had been cut, this difference was not significant. These findings underline the long-term impact of this invasive alien plant on natural ecosystems by increasing the soil N content over a long term.

Plant available P content was the highest in the former croplands in 2014 as result of former P-fertilisation, but after the abandonment, it started to decrease significantly. As P has a low mobility in soils, this decrease can be a result of the P consumption by the vegetation and soil microbes. In the grasslands and former plantations, P content was similarly low, in both cases low pH likely facilitated the mobilisation (Alt et al. 2011), i.e. leaching from topsoil. In former plantations and grassland, there were no temporal changes between the two sampling dates. The high N in the soils of former plantations and the high P availability in the soil of former croplands, should be considered as a relevant regulating factor in subsequent grassland recovery (Alt et al. 2011) and might hinder vegetation recovery for almost a decade (An et al. 2019).

Vegetation changes

We found that, four years after land use change, grassland vegetation was in an early or mid-successional stage, both on the mounds formerly used as cropland and forest plantation. The three vegetation types were clearly separated by their species composition (Figure 4). The recovering grasslands had a few common species with the reference grasslands and were mostly characterised by weed species. The indicator species of the recovering grasslands reflected the different site histories. On mounds, formerly covered by croplands, mostly weeds typical of former arable lands and fallows were present, such as *C. arvensis*, *L. perenne*, *T. arvensis* and *X. strumarium* (Table 3). Mounds, formerly covered by plantations, were characterised by weed species typical of the under-

storey of black locust plantations, such as *B. nigra*, *B. sterilis* and *G. aparine*. However, some weed and disturbance-tolerant species occurring also in dry grasslands were also present, such as *A. collina*, *V. arvensis* and *V. grandiflora*. The only indicator species on former croplands which is typical of undisturbed grasslands was *A. pratensis*. The latter is a typical competitor species of alkali meadows, but it can also cope with dry habitat conditions, thus, it often can be found in the loess grasslands of the region (Borhidi et al. 2012, Deák et al. 2014). Indicator species of mounds covered by grasslands were mostly species typical to alkali (*F. pseudovina*, *P. lanceolata* and *T. retusum*) and loess grasslands (*C. praecox*, *E. hispidus*, *E. virgata*, *K. cristata* and *S. nemorosa*) (Borhidi et al. 2012, Deák et al. 2014) (Table 3). Only a few weed species such as *B. hordeaceus* and *E. cicutarium* were present, likely due to moderate grazing (Godó et al. 2017).

Species composition of weeds reflected well the site history. Weeds are generally R-strategists and have a dense and persistent seed bank (Török et al. 2012; Melnik et al. 2017). Thus, even several years after the cessation of crop production and cutting of plantations, weed species were able to germinate from the seed bank. Contrarily, the usually K-strategist grassland species generally have a sparse and transient seed bank (Bossuyt and Honnay 2008), thus their seed bank is generally depleted even after a few years of improper management (Valkó et al. 2011). As the studied mounds were used as arable land or black locust plantation for decades, there was no possibility for the grassland species to recover from the seed bank. Another reason for the low proportion of grassland species on the recovering mound vegetation is the lack of dispersal vectors (Deák et al. 2016b). Even though semi-natural grasslands were present near the recovering mounds, the dispersal vectors (the grazing livestock) were missing. As many grassland plant species have a limited dispersal ability and thus a limited dispersal radius, lack of active dispersal vectors can considerably hinder their establishment, even in semi-natural landscapes (Jacquemyn et al. 2010; Auffret 2011). The results regarding the naturalness of the vegetation also suggested that vegetation recovery is at an initial stage even four years after land use change. The naturalness of the recovering vegetation was low in case of both former croplands and plantations (Figure 5). However, it is shown by the results of the GLMM that the vegetation recovery was more successful on former croplands compared to former plantations (Table 2). The proportion of species typical of natural habitats was significantly higher on mounds formerly covered by cropland than on mounds formerly covered by black locust plantation.

The reason for the low success of vegetation recovery on former plantations is the legacy of the former woody vegetation and forestry practices. For establishing a forest plantation, more drastic soil works are needed compared to arable use. Even though the soil works are not so frequent, such as in the case of arable use, they can affect the soil structure in deeper layers. Thus, it affects the chemical properties of the soil in a more intense way; furthermore, deep ploughing transports the seed bank of grassland species to such deep layers (even 1 m deep) from where they are not able to germinate and re-establish. Due to the shading effect of woody vegetation, a milder micro-climate is present in the understorey of the woody habitats (Tölgyesi et al. 2020), which affects their species composition. It could still be observed by the low cover-weighted cover of

LB and high WB scores of the vegetation. Another detrimental effect of black locust on dry grassland species is that, due to its nitrogen fixation, it considerably increases the nitrate content of the soil (Figure 3; and see also Cierjacks et al. 2013; Vítková et al. 2017). The increased residual nitrate content could even be observed four years after eliminating black locust trees (Table 1) and it had a considerable effect on the vegetation by decreasing the naturalness index (Table 3). The high nitrate content generally favours species adapted to ruderal habitats (low naturalness index) and suppresses stress-tolerant species adapted to dystrophic soil (Jentsch and Beyschlag 2003; Albert et al. 2014). Black locust is a species that can re-sprout very effectively after disturbance (Vítková et al. 2017). Under the studied climatic and edaphic conditions, only very few re-sprouting ramets were observed three years after the removal of *Robinia*. However, regular monitoring is needed to detect the abundance of black locust ramets and apply follow-up management, if necessary.

Conclusions

Our results suggest that the legacy of a former intensive land use (i.e. cropland and plantation) is more complex than the effect of excess soil nutrients. Even though former croplands were characterised by excess P and former plantations by excess N (Figure 3), the reasons for differences in vegetation characteristics are likely more complex. The long-lasting various disturbance regimes (fertilisation, herbicide application, tillage) typical for croplands, shading and altered microclimate typical for plantations and the deep cultivation typical for both, are the most likely legacies that hamper or slow down the grassland recovery in the studied habitats.

We found that, without proper management measures, recovery of grassland vegetation is slow on mounds formerly used as cropland or black locust plantation. This is in line with the findings of Török et al. (2011b), who found that a significant decrease in the proportion of the weeds can be expected approximately 10 years after cessation of croplands in the studied region. Our results suggest that arable use transformed the habitat conditions in a more moderate way than the establishment of plantations. Thus, restoration efforts, focused on the restoration of mounds formerly covered by arable lands, can be more effective compared to the restoration of mounds formerly covered by forest plantations. From a practitioner point, it should also be noted that costs associated with the elimination of woody vegetation is high. Especially if we take into account that, in many countries (like in Hungary), a high penalty (ca. 11000 euros per hectare) should be paid in case of elimination of a forest parcel (regardless of whether it is a native forest or an invasive plantation) or, alternatively, another forest of the same area has to be established elsewhere.

Even though spontaneous regeneration of grassland habitats can be a good solution in nature conservation practice, it might be risky as the vegetation development is often unpredictable. The outcome of spontaneous succession is highly dependent on initial site conditions, including land use intensity, landscape context, climatic

and edaphic factors. Spontaneous recovery is often unpredictable also due to the founder effect, i.e. that the vegetation composition of late successional phases strongly depends on the initial plant assemblages (Grime 1998). As in case of spontaneous succession, where the initial plant establishment processes have a random pattern, the outcome of the succession can be unfavourable from a nature conservation view or even can stack in a weed dominated phase (Deák et al. 2015; Albert et al. 2014). In case of spontaneously recovering former arable lands and forest plantations, the dense seed bank of the weed species might shift the vegetation development to undesirable pathways. In case of former plantations, resprouting of woody vegetation might also occur (Cierjacks et al. 2013). Thus, continuous monitoring of the spontaneously recovering vegetation is recommended. In case of unfavourable vegetation changes, further measures might be necessary, such as seed sowing of good competitor grassland species (Valkó et al. 2018).

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